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Observations on the Taxonomy and Range of *Hesperarion* Simroth, 1891 and the Evidence for Genital Polymorphism in *Ariolimax* Mörch, 1860 (Gastropoda: Pulmonata: Arionidae: Ariolimacinae)

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Abstract. A new terrestrial slug species, *Hesperarion* ***plumbeus,*** sp. nov., is described from Shasta County, California. It differs from other species of *Hesperarion* in its leaden gray body color and in details of the reproductive system. The anatomy of *Hesperarion mariae* Branson, 1991, is redescribed, including the presence of a dart sac and long calcareous dart. Its range is extended to central western Oregon. Newly recorded localities for *Hesperarion niger* (Cooper, 1872) document a wider range for the species in northern California. Auxiliary copulatory structures equipped with calcified darts in *H. mariae* and *H. niger* call into question the assignment of these and other ariolimacine taxa to Arionidae. *Gliabates oregonius* Webb, 1959, is probably not an ariolimacine slug but may be assignable to Milacidae. A hemiphallic condition reported in at least three species of *Ariolimax* is probably a genital polymorphism and not the result of apophallation.

INTRODUCTION

The western North American terrestrial slug taxon *Hesperarion* Simroth, 1891, has been known to include three species, the type-species, *Hesperarion niger* (Cooper, 1872); *H. hemphilli* (W. G. Binney, 1875), and *H. mariae* Branson, 1991. Over the past few years, I have accumulated new information on *Hesperarion* from several sources, including (1) a new species with an apparently restricted range in northern California; (2) extensions of known range and additional morphological data on *H. mariae*; (3) additional range information on *H. niger* in the Klamath/Siskiyou region; and (4) the presence of calcareous darts in the reproductive system of at least some species.

In describing the monotypic genus *Gliabates,* Webb (1959) compared its type-species, *G. oregonius,* to *Hesperarion hemphilli.* Because the brief and incomplete original description gives the impression that *G. oregonius* might be congeneric with or similar to *Hesperarion,* and to rule out the possibility that *G. oregonius* was the same species as ***H. plumbens***, sp. nov., described below, I reviewed the evidence for such a relationship. *Gliabates oregonius* is probably not an ariolimacine slug but may be assignable to Milacidae.

The presence in some apparently sexually mature specimens of the several species of *Ariolimax* Mörch, 1860, of a diminutive male genital tract without the characteristic terminal copulatory organs has been attributed to apophallation—the bizarre sexual behavior in which at the end of copulation one slug chews off the penis of its mating partner. However, apophallation does not seem adequate to explain the observed hemiphallic condition (hemiphallic: with reduced, but not absent, male genitalia), and I argue here that there may instead be an unrecognized genital polymorphism in at least three of the nominal taxa of *Ariolimax.* The resolution of this question is significant, because the reproductive biology of *Ariolimax* species has been the topic of numerous studies and considerable theorizing (see Leonard et al., 2002).

MATERIALS AND METHODS

The following abbreviations are used: ANSP, Academy of Natural Sciences, Philadelphia; BR, author's collection, San Francisco, California; CAS, California Academy of Sciences, San Francisco; SBMNH, Santa Barbara Museum of Natural History; DEIX, collection of Deixis Consultants, Seattle, Washington; S-TNF, reference collection of Shasta-Trinity National Forest, Redding, California.

Species concept: Most land mollusk taxonomy over the past 60 or 70 years has been practiced ostensibly with reference to the "Biological Species Concept" (Mayr, 1940)[1] or its immediate predecessors (e.g., Dobzhansky, 1937; see, for example, Pilsbry, 1939:xiv). In practice, observations of presence or absence of interbreeding have rarely been attempted. More often, the judgment of what

[1] "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr, 1940). For additional critiques of the concept, and reciprocal criticism of phylogenetic species concepts, see Wheeler & Meier (2000).

is a particular land snail or slug species has been based on degree of difference criteria and the distribution of character states through an array of specimens, or on other circumstantial evidence of reproductive isolation such as differing genital morphology.

For purposes of this report, *a species comprises all the individual organisms predicted on the basis of available evidence to prove to compose a least inclusive monophyletic unit recognized in a formal phylogenetic analysis.* It is expected that upon such analysis this aggregation of individuals will conform to the species concept of Mishler & Theriot (2000), grouping together as a taxon because of evidence of monophyly. The relevant evidence of monophyly is apomorphic character states. This definition generates a hypothesis about the way such an analysis will turn out. The result of a phylogenetic analysis is itself a hypothesis about the true historical relationships among its taxa. Because for most clades of North American land mollusks, species-level phylogenetic analysis has not yet been performed, this is a "working" definition. But I believe taxa thus recognized will prove the most useful units for estimates of biodiversity, ecological studies, conservation and management decisions, and other end uses of taxonomy.

The taxonomy of North American land mollusks inherited from Pilsbry (1939–1948) and his successors includes numerous subspecies, also recognized on degree of phenetic difference, subjectively judged.[2] There is no generally agreed-on rule regarding their formal taxonomic recognition, and for reasons articulated by Wilson & Brown (1953) there are unlikely to be any. I agree with proponents of phylogenetic species concepts (e.g., Mishler & Theriot, 2000; Wheeler & Platnick, 2000) that the least inclusive taxon in formal taxonomy should be the species, and that where they exist, well defined, diagnosable "subspecies" should simply be called species. What is "well defined" remains a taxonomist's judgment call, but arbitrary decisions on rank are less a factor than before. With improved methods of study, many western North American taxa formerly ranked as subspecies have been shown to have attributes such as genital differences that mark them as species even under the Biological Species Concept (Roth & Miller, 1993, 1995).

SYSTEMATICS

Arionidae Gray in Turton, 1840

Ariolimacinae Pilsbry & Vanatta, 1898

Hesperarion Simroth, 1891

Type species: *Ariolimax niger* Cooper, 1872, by original designation.

[2] "Most subspecies are recognizably differentiated populations which are not considered sufficiently distinct to be called species" (Pilsbry, 1939:xiv). "In ambiguous situations it is . . . advantageous to treat allopatric populations of doubtful rank as subspecies" (Mayr, 2000:26).

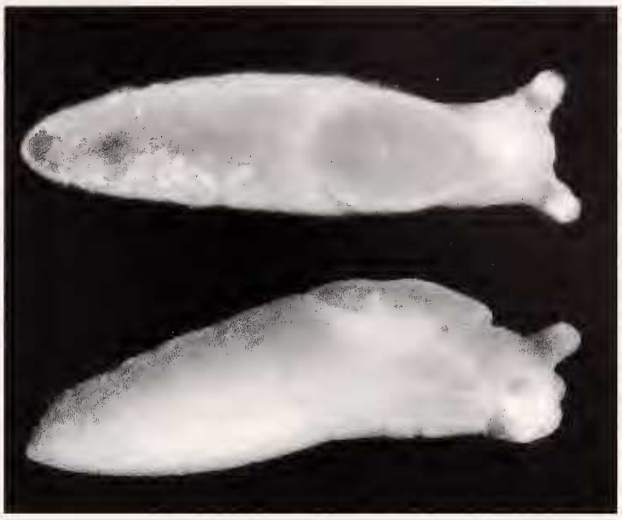


Figure 1. *Hesperarion* ***plumbeus*** Roth, sp. nov., holotype, SBMNH 350346. Dorsal and right latero-ventral views. Length in alcohol 12.1 mm.

Ariolimacinae with body one-colored or maculated, without bands but often with scattered small spots or rosettes of darker pigment. Pneumostome behind midpoint of mantle. Dorsum behind mantle keeled. Back and sides covered with network of impressed grooves. Foot fringe prominent, crossed by vertical stripes. Buccal and tentacular retractor muscles originating close together at rear margin of floor of lung. Retentor muscle absent. Epiphallus slender throughout its length, inserting on domed or flattened summit of penis; penis containing a verge. Appendix sometimes present on lower part of atrium. Dart sac with single or multiple darts present or absent. Spermatophore produced. Internal shell a low-arched plate with off-center terminal nucleus.

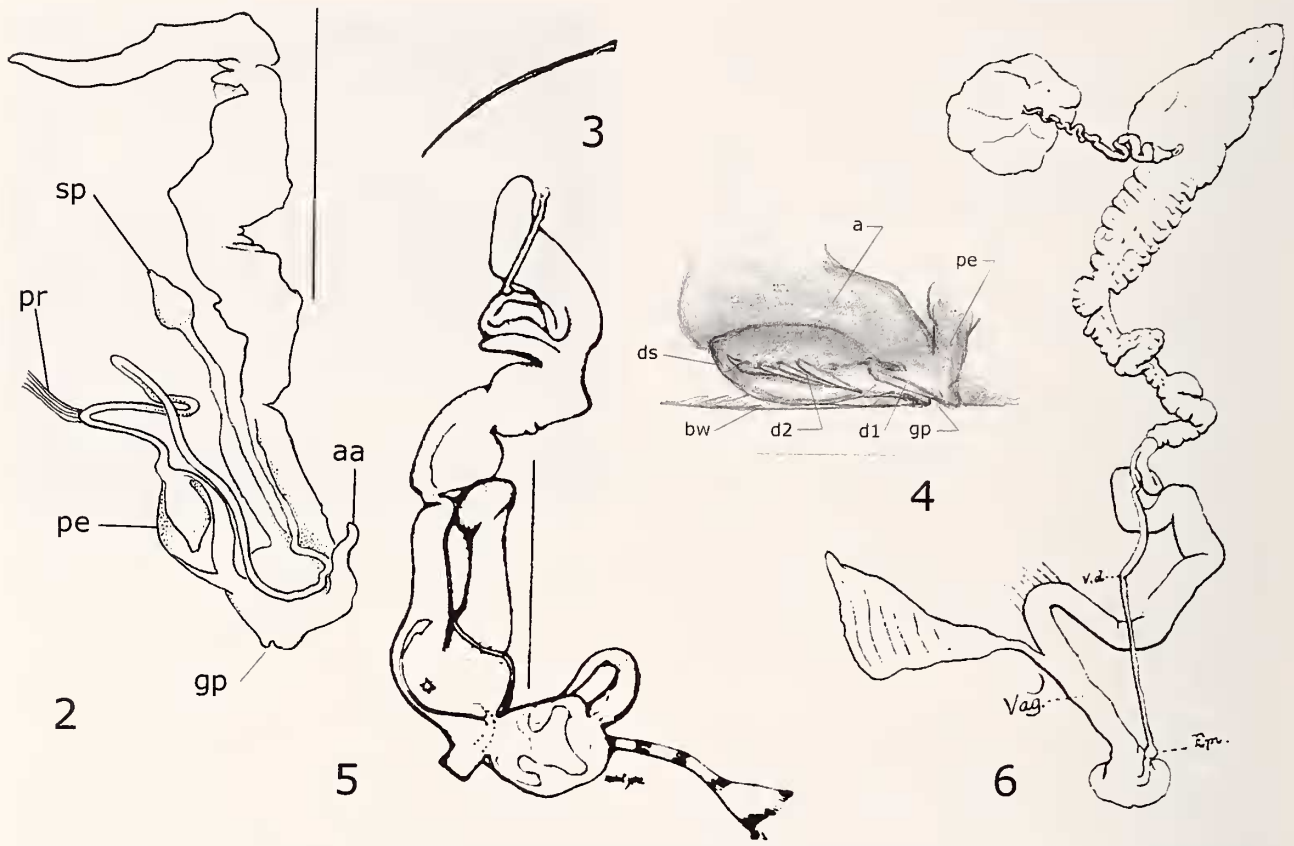
The genus ranges from Tillamook County, Oregon, to Orange County, California. Four species are known.

Hesperarion ***plumbeus*** Roth, sp. nov
(Figures 1, 2)

Hesperarion, new species "p" Roth & Sadeghian, 2003:45.

Diagnosis: A small *Hesperarion* with body color predominantly gray, not spotted; foot fringe lacking prominent stripes; verge teardrop-shaped; atrium with appendix; spermathecal duct long.

Description: Extended length 1.5–2 cm. Body color leaden gray in living specimens, grayish brown in alcohol, somewhat lighter on the sides and neck; lacking darker spots or rosettes of pigment. Mucus grooves very slightly darker than adjacent skin. Mantle of same ground color as rest of dorsum, with faintly darker mottling. External genital pore immediately posterior to right ocular tentacle. Foot fringe pale tan to gray, not obviously striped,



Figures 2–6. Figure 2. *Hesperarion* ***plumbeus*** Roth, sp. nov. Reproductive system, based on paratype SBMNH 350347. aa, atrial appendix; gp, external genital pore; pe, penis (opened to show verge); pr, penial retractor muscle; sp, spermatheca. Scale line = 2 mm. Figure 3. *Hesperarion mariae* Branson, 1991. Calcareous dart from reproductive system. BR 2383, Oregon: Lane County. Length approx. 2 mm. Figure 4. *Hesperarion niger* (Cooper, 1872) (?). Author's sketch of dart sac and atrium; dorsal view, anterior to right. CAS 085856, California, Sonoma County: Stuart Canyon, along canyon trail, S side of Stuart Creek, E of Glen Ellen. a, atrium; bw, body wall of right side of animal; d1, dart extending close to genital pore; d2, additional darts farther back in sac; ds, dart sac; gp, external genital pore; pe, penis. Scale line = approx. 2 mm. Figure 5. *Gliabates oregonius* Webb, 1959. Original illustration of reproductive system of holotype in Webb collection (Webb, 1959:28, fig. 37) Scale line = 2 mm. Figure 6. *Ariolimax columbianus* (Gould in A. Binney, 1851) (?). Original illustration of reproductive system of *Aphallarion buttoni* Pilsbry & Vanatta, 1896 (Pilsbry & Vanatta, 1896:pl. 14, fig. 12). Size not stated in original.

sometimes slightly darker for posterior 10% of length and anterior 10–15%. Sole uniform, light tan. Mantle about 30% of length of preserved animal. Caudal mucus pore prominent. Medial row of dorsal tubercles slightly more prominent than remainder, colored like the rest or slightly lighter posteriorly, overhanging caudal mucus pore.

Penis short, with swollen summit, containing teardrop-shaped verge, smaller than cavity of penis. Retractor muscle present; inserted at vertex of first hairpin bend of epiphallus above summit of penis; strap-shaped. Vas deferens long, slender, convoluted near middle of its length. Atrium with small appendix, broad below, tapering to vermiform tip. Spermathecal duct inserting on atrium next to free oviduct, moderately long, upper 40% of length somewhat more slender than lower 60%; spermatheca small, acorn-shaped.

Type material: Holotype, SBMNH 350346, **CALIFORNIA:** *Shasta County*: Castle Creek, 1.3 km WNW of junction with South Fork Castle Creek, 41.153°N, 122.406°W, D. Sager coll. 11 June 2000.

Paratypes: SBMNH 350347, same locality and collection data as holotype (1 specimen). BR 2348, Shasta County: Root Creek about 2.4 km NW of junction with Castle Creek, 41.163°N, 122.396°W, K. Piper coll. 12 April 2000 (1).

Remarks: *Hesperarion* ***plumbeus*** resembles *H. niger* (Cooper, 1872) in the presence of a broad-based but otherwise slender caecum on the atrium, opposite the insertion of the penis. The penis is proportionally shorter than that of *H. niger* and less blunt at the summit; the verge is teardrop-shaped rather than broadly conical. *Hespera-*

rion niger and *H. **plumbeus*** are sympatric in the region of Root Creek (see below under localities for *H. niger*).

*Hesperarion **plumbeus*** could possibly be confused with an unnamed species of *Prophysaon* Bland & W. G. Binney, 1873, similar to *P. coeruleum* Cockerell, 1890, which is of similar size and coloration and occurs along some streams in extreme northern Siskiyou County, California. In *Prophysaon,* however, the pneumostome is located anterior to the midline of the mantle and the tail lacks a prominent mucus pore.

Etymology: Latin, *plumbeus,* made of lead, leaden.

Hesperarion mariae Branson, 1991 (Figure 3)

Hesperarion mariae Branson, 1991:109–110, figs. 1, 2.

Revised description: Extended length 3 cm. Body ground color light reddish gray, somewhat lighter on sides; with small, black "spider-web" spots; spots sometimes aligning along mucus grooves of flanks, but not joining in reticulation. Mantle of same ground color as rest of body. Head and cephalic tentacles somewhat darker than rest of body. Sole white, unmarked. Foot fringe prominent, crossed by alternating light and dark stripes. Internal shell a low-arched plate with off-center terminal nucleus; periostracal margins extending beyond calcified part of shell. Caudal mucus pit present.

Penial retractor muscle strap-shaped, inserted at summit of penis. Penis cylindrical, with blunt summit; containing a verge. Verge broadly conical, nearly filling cavity of penis. Atrium with thin-walled, capacious sac containing single long, curved, calcareous dart with sharp tip and slightly expanded base (Figure 3).

Referred material: OREGON: *Lane County*: [Specific locality not stated], J. S. Applegarth coll. 9 January 1996 (BR 2383; 1 specimen). Big Canyon Creek, 43.983°N, 123.642°W, J. S. Applegarth coll. 26 July 1995 (BR 1900; 1 specimen). Mouth of Big Canyon, 43.983°N, 123.642°W, old log bridge, J. S. Applegarth coll. 25 August 1995 (BR 1893; 1). *Douglas County*: along S side of Footlog Creek, 43.642°N, 123.867°W, T. J. Frest, E. J. Johannes coll. 30 October 1998 (DEIX loc. 3945; 1 specimen)

Branson (1991) described the new species *Hesperarion mariae* from two specimens collected at Cape Lookout, Tillamook County, Oregon (45.340°N, 123.992°W). On 23 August 1997 I collected two specimens of *H. mariae* from under debris on the ground in Sitka spruce woods with sword fern and mixed shrub understory at the type locality. These specimens (BR 2027) were subsequently lost in a laboratory (actually, kitchen) accident, but not before I was able to compare them to the material from Lane County and establish that all the specimens were conspecific.

Remarks: Although Branson stated that *H. mariae* was "most closely related to" *Hesperarion hemphilli,* his comparisons among the three nominal species were brief, especially with regard to the reproductive system anatomy that is diagnostic of species in *Hesperarion* (cf. Pilsbry, 1948). He made no reference to the presence of a dart sac or dart. Unless he overlooked it, the absence of dart apparatus in the type material of *H. mariae* may be developmental, as is suggested below for *H. niger.*

Branson (1991:110, fig. 2) described and illustrated a peculiar downward deflection of the tail tip of the holotype of *H. mariae.* This appears to be a preservational artifact. In some preserved specimens I have examined, the posterior end of the sole folds longitudinally into the caudal pore with the result that the tip turns slightly downward. Branson's (1991:109) description of the body being "raised in a hump beneath the mantle" is another preservational artifact, sometimes seen in other *Hesperarion* species as well.

Hesperarion niger (Cooper, 1872) (Figure 4)

Ariolimax niger Cooper, 1872:147, pl. 3, figs. E, 1–4.
Hesperarion niger (Cooper), Pilsbry, 1948:723–726. Roth & Pressley, 1983:73–77. Roth & Sadeghian, 2003:45.

Revised description: Extended length 3–5 cm. Body blackish brown to reddish gray, somewhat lighter on the sides, with numerous small, irregular, black spots scattered over surface, some joining in oblique reticulation along mucus grooves of flanks. Mantle of same ground color as rest of body. Foot fringe tan to gray, vertically striped with black. Sole uniform, white to light tan, unmarked or with two longitudinal rows of black spots defining lateral zones. Internal shell a low-arched plate with off-center terminal nucleus; periostracal margins extending beyond calcified part of shell. Caudal mucus pore prominent. Penis cylindrical, with blunt summit, constricted at base. Penial retractor muscle broad, strap-shaped, inserted at summit of penis. Verge broadly conical, much smaller than cavity of penis. Vas deferens long, slender, convoluted near middle of its length. Epiphallus entering summit of penis, of uniform diameter throughout. Atrium containing three massive pilasters, with either appendix present at base, broad below and tapering to vermiform tip, or else or broad sac on right side, containing multiple, tusk-shaped calcareous darts. Free oviduct as long as or moderately longer than vagina.

Revised distribution: Roth & Pressley (1983) reported *H. niger* from rockslides in the vicinity of Big Bar, Trinity County, California (40.741°N, 123.255°W), an extension of known range approximately 195 km from Williams, Colusa County, California. This was the northernmost accurately located locality known for the species at the time. However, in his original description of the species, Cooper (1872) had surmised that a specimen mentioned by Gould (1852), questionably from Oregon, might be

conspecific. The Oregon specimen may have been *H. mariae,* which is colored like some specimens of *H. niger.*

The following additional localities document a more extensive range for *H. niger* in northern California: *Shasta County*: Root Creek about 2.4 km NW of junction with Castle Creek, 41.163°N, 122.396°W, K. Johnson coll., 12 April 2000 (S-TNF Derby H-4; 1 specimen). Reynolds Basin near Pit River Arm of Shasta Lake, 40.971°N, 122.019°W, K. Johnson coll. 18 April 2000 (BR 2288; 1); 19 April 2000 (S-TNF RE 112-4a; 1). *Humboldt County*: Whiting Ridge about 0.5 km SW of Pilot Creek head, 40.675°N, 123.635°W, K. E. Schlick coll. 3 November 1998 (BR 2129; 1). *Glenn County*: N face of Tool Cache Ridge above S Fork Elk Creek, 39.564°N, 122.646°W, U.S. Bureau of Land Management personnel coll. 6 April 1999 (BR 2197; 1).

Remarks: CAS 085856 (**CALIFORNIA:** *Sonoma County*: Stuart Canyon, along canyon trail, S side of Stuart Creek, E of Glen Ellen, 38.368°N, 122.498°W, E. J. Kools coll. 10 December 1992; 1 specimen) conforms to the above description and largely to other literature accounts of the species, but instead of a broad-based but otherwise slender caecum on the atrium, opposite the insertion of the penis, it has a large atrial sac containing four or more tusk-shaped, hollow, calcareous darts (Figure 4). All adhere by their bases to the interior wall of the sac. The most anterior dart extends almost to the exterior genital pore; it is slightly separated from the more posterior darts, which lie in a row farther back in the sac.

Auxiliary copulatory structures equipped with calcified darts are known in Helicoidea, Gastrodontoidea, Ariophantidae, Parmarionidae, Philomycidae, and Urocyclidae (Tompa, 1980; Gómez, 2001). This and the occurrence in *H. mariae,* above, are the first records of darts in taxa assigned to Arionidae. However, they also suggest that the traditional assignment (e.g., Pilsbry, 1948) of Ariolimacinae and diverse other western North American slug taxa to Arionidae may need re-examination.

(?) Milacidae Ellis, 1926

Gliabates Webb, 1959

Type species: *G. oregonia* [*sic*] Webb, 1959, by monotypy.

In describing the monotypic genus *Gliabates,* Webb (1959:22–23, 28) compared its type-species, *G. oregonius,* to *Hesperarion hemphilli.* Because the brief and incomplete original description gives the impression that *Gliabates oregonius* might be congeneric with or similar to *Hesperarion,* and to rule out the possibility that *G. oregonius* was the same species as *H. **plumbeus,*** I reviewed the evidence for such a relationship.

The type-species of *Gliabates* Webb, 1959, is *G. oregonius* Webb, 1959, described in the same paper.[3] The type locality is **OREGON:** *Lane County*: east bank of Long Tom River, adjacent to Alderwood State Park, on road [= Oregon State Highway] 36, near Cheshire (44.190°N, 123.277°W). Webb (1959:22) compared several points of the anatomy of *G. oregonius* to *Hesperarion hemphilli.* Although he stated, "the writer believes the retention of *Hesperarion hemphilli* (W. G. Binney) in *Hesperarion* is faulty," he did not explicitly assign *H. hemphilli* to *Gliabates.* The new genus was therefore monotypic.

Webb's (1959:28) original figure of the genitalia of *G. oregonius* (reproduced here as Figure 5) shows a broad, blunt-topped penis inserting low on the atrium. A conical epiphallus much more slender than the penis inserts subcentrally on the penial summit. A penial retractor muscle inserts on the penial summit adjacent to the epiphallus. The retractor muscle is narrow at its insertion, widening fanlike away from the penis. The cavity of the penis is divided internally into an upper and a lower part by a collar; the division is weakly marked externally by a faint constriction. The summit of the penial cavity bears a low, broad papilla.

The atrium is large and apparently nearly filled by the thickened mediad wall through which the duct of the spermatheca opens into the atrial cavity. The spermatheca is ovoid, smaller than the penis, with a thick-walled stalk that is nearly as large in diameter as the spermatheca itself. The free oviduct is long and tubular.

This genital morphology is similar to that of *Milax* Gray, 1855, of Milacidae; see, for example, Wiktor (1987:163–164, fig. 15). A broad, blunt-topped penis is characteristic of most species of *Milax,* although the overall shape varies from species to species. The epiphallus in *Milax* is typically well differentiated from the penis. It is usually more slender than the penis, often strikingly so. Its shape varies, being cylindrical, conical, or club-shaped. The penial retractor muscle usually inserts adjacent to the epiphallus. A papilla is present in the penis. The penis is sometimes divided by constrictions into two or more parts. The spermatheca varies in shape but its stalk is usually thick.

Inside the atrium of *Milax* there are usually one or more "stimulators" of different shapes, often specific to a species (Wiktor, 1987:178). The stimulators originate on the atrial wall on the spermathecal, rather than the penial, side of the cavity, where *Gliabates oregonius*

[3] The original description of *Gliabates* is as follows: "*Gliabates,* New genus: Approximating *Hesperarion* as typified by *H. niger* Cooper, but without a definite verge in the upper part of the penis below the insertion of a short epiphallus. Penis with upper and lower cavities formed by a lobeate [*sic*] collar-like suggestive of the organ of *Allogona* or *Euchemotrema* of the *Polygyridae.* Vagina and basal spermathecal duct expanded and perhaps eversile, but lacking accessory organs" (Webb, 1959:22; italics as in original).

shows a thickened atrial wall. In *Milax* the atrium is served by an atrial accessory gland; Webb (1959) did not report or illustrate any such gland in *G. oregonius*.

No dart apparatus is present in *G. oregonius* (Roth, 1996; G. R. Webb, written communication, 1990). *Hesperarion hemphilli* differs from *G. oregonius* in having a large, conical verge that fills much of the penial sac and is asymmetrically grooved on one side. The penis is ovoid (Pilsbry, 1948:figs. 391a, 392a) or somewhat conical (CAS 029771, **CALIFORNIA:** *Alameda County*: Niles, now a district of city of Fremont, about 35.58°N, 121.98°W, H. Hemphill coll.; 8 specimens). The epiphallus is relatively thicker, widening above its insertion on the penis so that the transition is not abrupt as in *G. oregonius*. *Hesperarion hemphilli* is usually reported not to have an appendix on the atrium (and to differ in this respect from *H. niger*); but in CAS 029772 (**CALIFORNIA:** *San Mateo County:* Tunitas Canyon, 8 mi [12.8 km] S of Half Moon Bay, about 37.36°N, 122.39°W, W. H. Lange, Jr. coll. 5 March 1940; 1 specimen) the atrium bears a small, knoblike basal sac. Similarities of *H. hemphilli* to *G. oregonius* include a broad, thick-walled duct of the spermatheca and thickening of the atrial wall opposite the penis.

EVIDENCE FOR A HEMIPHALLIC, NOT APOPHALLATE, PHASE IN *ARIOLIMAX*

Apophallation, the behavior in which one slug chews off the penis of its mating partner, has long been noted in species of *Ariolimax* (Heath, 1916; Mead, 1943; Pilsbry, 1948; Leonard et al., 2002), although not always accurately reported (Reise & Hutchinson, 2002). It was first illustrated by Harper (1988). Apophallation has been invoked to explain the presence, in some apparently sexually mature specimens, of a diminutive male genital tract without the elaborate penis, verge, and epiphallus characteristically observed in the several species. However, apophallation, the traumatic severing of replete organs, does not seem competent to produce this incompletely phallic (but fully "connected") condition. Here is a chronology of the intellectual development of the concept, followed by a critique and the evidence for male genital polymorphism.

Chronology

1896 Pilsbry & Vanatta (1896:348, ff.) described the new genus and species *Aphallarion buttoni,* based on specimens from Oakland, California, said to have characters as in *Ariolimax* but lacking a penis and penial retractor and instead having a small, short epiphallus. Their figure of the genitalia (op. cit.:pl. 14, fig. 12; reprinted by Pilsbry, 1948:fig. 286K, and here as Figure 6) shows a simple lower male genital tract extending from the vas deferens to the base of the atrium, of almost uniform diameter except for a small swelling identified as the epiphallus ("Epi").

1916 Heath (1916; quoted by Pilsbry, 1948:710–711) observed that about 5% of *Ariolimax californicus* Cooper, 1872, dissected in his classroom lacked a penis and in another 5% it was "abnormally undeveloped when compared with that of smaller individuals which had not yet reached sexual maturity." He described the act of apophallation and the dissection of four individuals (two pairs?) that had engaged in (reportedly unilateral) copulation followed by apophallation.

Circa 1916 Heath and Pilsbry corresponded and agreed that *Aphallarion* represented individuals of *Ariolimax* that had undergone apophallation (Pilsbry, 1948:711).

1941 Waste (1941:42–43) believed that *Aphallarion* represented individuals of *Ariolimax* that had undergone apophallation and cited a 1939 letter from Pilsbry to that effect. Waste stated that he had dissected specimens from Oakland and found them all to be *Ariolimax columbianus* (Gould in A. Binney, 1851). He further stated that he had found apophallation (i.e., hemiphallic individuals?) in *A. californicus* in which "the abnormality greatly resembles Pilsbry's [*sic*] figure (except for specific differences in the penile retractor)."

1943 Mead (1943) accepted apophallation as the explanation for the condition described in *Aphallarion buttoni.*[4] He found normal specimens of *A. columbianus* at Oakland, co-occurring with hemiphallic individuals and concluded that *Aphallarion buttoni* represented apophallated *A. columbianus.*

1948 Pilsbry (1948:706–711) repeated the synonymy of *Aphallarion* with *Ariolimax* and of *Aphallarion buttoni* with *Ariolimax columbianus* and quoted text from Heath and Mead supporting apophallation as the explanation for hemiphallic individuals.

Discussion

Apophallation, as described by Heath (1916) and Leonard et al. (2002) and illustrated by Harper (1988) would not directly produce a configuration such as that shown by Pilsbry & Vanatta (1896) for *Aphallarion buttoni.* In

[4] "Apophallation alone accounts for most of the differences which Pilsbry and Vanatta found" (Mead, 1943:685).

that figure, the lower male genital tract extends without interruption from the branching off of the vas deferens from the oviduct to its insertion on the lower atrium, near the external genital pore (Figure 6). Apophallation would produce an unfilled gap from somewhere upstream from the epiphallus to near the external genital pore; all the structures contained in the everted penis (see Mead, 1943: pl. 2, fig. 12) would have to be severed for the penis to come away free.

The drawing of *Aphallarion buttoni* instead resembles an intact individual (probably of *A. columbianus,* as Mead diagnosed based on other features of the anatomy, and as the known distribution of *A. columbianus* tends to confirm) that has not attained the usual replete condition of the lower male sperm-delivery organs. Reproductive ductwork in pulmonate land mollusks starts out as simple slender tubes that only later in ontogeny develop their various elaborations. However, the rest of the reproductive system in the figure of *A. buttoni* looks like that of a sexually mature individual.

The original lot of slugs from Oakland that Pilsbry and Vanatta received from F. L. Button still exists at the Academy of Natural Sciences, Philadelphia (ANSP A7039) and contains 58 specimens (Paul Callomon, personal communication, 2002). It is not clear that Pilsbry and Vanatta dissected more than one specimen. All other authors have found *Ariolimax* specimens from Oakland to be *A. columbianus,* and it is possible that some proportion of the specimens in this original lot, if dissected, would prove to have the usual *columbianus* genitalia.

Heath's (1916) report of dissecting apophallated *A. californicus* does not make sense. He reported the position of the severed allo-penis lodged in the female tract of the recipient (interestingly, with its end in the bursa copulatrix), where it was held tightly by what probably was the intrinsic muscle of the vagina.[5] Then he stated that "*in the other two specimens* the penis was wholly absent, and the vas-deferens extended *to the genital pore*" (emphasis supplied). But this description must pertain to the autopenes of the dissected specimens that contained the severed penes—not to the apophallated individuals. In other words, the non-apophallated individuals had genitalia resembling the figure of *Aphallarion buttoni.* Heath himself reported that copulation was non-reciprocal—so these individuals might not have everted their penis in that copulation, even if they had had one to evert. We thus have reports in both *A. columbianus* and *A. californicus* of individuals with small, simple, lower male ducts. And in *A. californicus,* at least, such individuals engage in copulation.

There is evidence that *Ariolimax dolichophallus* Mead, 1943, may also have a similar hemiphallic configuration. Mead (1943:685) quoted A. G. Wetherby (author of an unavailable species-name, "*Ariolimax columbiana* var. *hecoxi*") to the effect that he had seen specimens from Santa Cruz, California, with genitalia like those of *Aphallarion buttoni.* The only species known to occur at Santa Cruz is *A. dolichophallus* (Mead, 1943; Leonard et al., 2002), so that must have been the species that Wetherby had.

Another reason to think that the hemiphallic state is not simply the juvenile condition in *Ariolimax* is Heath's report in a letter to Mead (quoted by Mead, 1943:685) of a sample of over 400 (!) specimens from Hog Island, Tomales Bay, Marin County, California, in which all of the specimens lacked a penis. It seems unlikely that the entire population of a perennial species would consist of juveniles. (Mead later visited Hog Island and found no slugs.) But it is plausible that an isolated population on a small island could be monomorphic for one state of a genital polymorphism, either from founder effect or, if the character is labile, from conditions that favored an extreme ratio of hemiphallic to phallic individuals.

The above considerations suggest that in at least three taxa of *Ariolimax* there are individuals that never develop replete lower male reproductive structures. They may engage in sexual encounters (although whether functioning as sperm donors as well as sperm recipients is not clear). In certain circumstances, a hemiphallic phase may be predominant in a population.

It does not seem likely that hemiphallic specimens represent individuals that have been apophallated and regrown male organs. The diminutive male genital tracts of hemiphallic specimens are smaller than the ducts that would be left behind after apophallation. Observations by Brooke L. W. Miller have indicated that apophallated male genitalia do not grow back, at least within a year (Miller, personal communication, 2003; and http://www.biology.ucsc.edu/grad/weaver/).

Although apophallation has been observed in *A. californicus* and *A. dolichophallus,* I have not located any observations of the same behavior in *A. columbianus.* If it does not happen in that species, then it cannot be the cause of hemiphallic individuals such as those on Hog Island or in Oakland.

Over 99% of euthyneuran gastropods are hermaphrodites, but a few stylommatophoran pulmonates have genitalia in which the male system is absent (aphally) or greatly reduced (hemiphally) (Tompa, 1984; Heller, 1993). Phallic polymorphism occurs in a few groups, including valloniid snails (*Vallonia* Risso, 1826; Gerber, 1996), pupilloid snails (*Columella* Westerlund, 1878; Pokryszko, 1987a; *Vertigo* Müller, 1774; Pokryszko, 1987b, 1990), agriolimacid slugs (some species of *Deroceras* Rafinesque, 1820; Pilsbry, 1948), and gastrodontid snails (*Zonitoides* Lehmann, 1862; Watson, 1934; Jordaens et al., 2001). The distribution and genetics of this type of polymorphism are the focus of considerable re-

[5] "The walls of the oviduct were in a high state of contraction" (Heath, 1916); what Heath referred to as the proximal section of the oviduct, more recent terminology would call the vagina..

search (Backeljau et al., 2001). It is tempting to speculate that, were it not for the drama of apophallation behavior, the observations of genital configurations in *Ariolimax* cited above would have been interpreted simply as another instance of phallic polymorphism in a pulmonate group.

The hypothesis of male genital polymorphism in *Ariolimax* can be tested by dissection of samples known not to have engaged in apophallation. Alternatively, and more appealing because it involves less sacrifice of specimens, it may be possible to inject an "erecting" hormone (APGWamide) that causes slugs to evert their genitalia (Brooke L. W. Miller, personal communication, 2002).

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